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Darwin wasps (Hymenoptera, Ichneumonidae) in Lower Eocene amber from the Paris basin

Alexandra Viertler[1,2*], Seraina Klopfstein[1,2*], Corentin Jouault[3,4,5], Tamara Spasojevic[1,2*]

1 *Naturhistorisches Museum Basel, Augustinergasse 2, CH-4001 Basel, Switzerland* **2** *Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland* **3** *Institut de Systématique, Évolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, CP50, 57 rue Cuvier, 75005 Paris, France* **4** *Institut des Sciences de l'Évolution de Montpellier, CNRS, Place Eugène Bataillon, UMR 5554, 34095 Montpellier, France* **5** *Univ. Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France*

Corresponding author: Tamara Spasojevic (spasojevic.ta@gmail.com)

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Abstract

Despite their ecological importance, Darwin wasps (Ichneumonidae) are among the most poorly studied groups of organisms. It is therefore not surprising that their fossil record is even more poorly understood than their extant diversity. The early Eocene seems rather fossil-poor regarding Ichneumonidae in amber and only one species, *Palaeometopius eocenicus* Menier et al., 2004, was described so far from Oise Amber from the Paris basin. Here, two new ichneumonid genera and species, *Madma oisella* **gen. et. sp. nov.** and *Pappous trichomatius* **gen. et. sp. nov.** are described and the placement of *Palaeometopius eocenicus* is revised. The three fossils are well-preserved and might represent stem taxa of Tryphoninae and Phygadeuontinae. They are a highly important addition to the early Palaeogene fossil record of Ichneumonidae that otherwise mainly consists of compression fossils, which yield far less detail of the specimens' morphology than amber pieces. Among the more than 1,000 Oise amber pieces examined, only three Ichneumonidae specimens have been found, versus about 60 Braconidae, a ratio very different from other amber deposits. Identification of additional ichneumonid specimens from this period (lowermost Eocene) is of particular importance for a better understanding of the subfamily and species compositions of this family after the K-Pg mass extinction.

* These authors contributed equally.

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Keywords
Amber deposit, Cenozoic, fossil, new genus, new species, Oise amber, parasitoids, plesiomorphic

Introduction

With around 25,000 described species (Yu et al. 2016) and between 60,000 and 100,000 estimated (Townes 1969; Rasnitsyn 1978), Ichneumonidae or "Darwin wasps" (Klopfstein et al. 2019) constitute one of the most diverse animal groups today and the largest family of parasitoid wasps . How these numbers compare to the past diversity of this group is largely unknown due to the poorly studied fossil record. In total, only 300 fossil species have been described, mostly from a few rather well-studied fossil localities, such as the latest Eocene Florissant Formation, which hosts one third of the known fossil species (PaleoBioDB 2021). This bias translates directly into a temporal bias in the ichneumonid fossils record, with more than half of the species known from the Eocene. Finally, the fossil record is strongly biased towards compression fossils, with only 31 species described from amber, most of which from the relatively poorly dated Baltic amber (for dating issues, see Sadowski et al. 2017).

The age of Darwin wasps has been estimated to the Early Jurassic, around 180 Ma (Spasojevic et al. 2021), but the oldest fossils are known from the Early Cretaceous (Kopylov 2009), resulting in a ghost lineage of around 60 Ma. The current evidence suggests that the Cretaceous ichneumonid fauna was dominated by extinct subfamilies, the earliest of which have been described from compression fossils: Tanychorinae, with uncertain placement in Ichneumonidae or Ichneumonoidea (Sharkey and Wahl 1992; Kopylov 2010a) and Palaeoichneumoninae (Kopylov 2009), the earliest unequivocal ichneumonids. Both subfamilies have been described from the Early Cretaceous of Transbaikalia and Mongolia. The more recently described Late Cretaceous subfamily Novichneumoninae is known from Burmese amber (Li et al. 2017; Kopylov et al. 2021), while Labenopimplinae have been described from the Late Cretaceous both from compression fossils from the Russian Far East (Kopylov 2010b), Botswana (Kopylov et al. 2010), Canadian (McKellar et al. 2013), and Taimyr amber (Kopylov 2012). Canadian amber also hosts the only Cretaceous ichneumonid described in an extant subfamily, *Albertocryptus dossenus* McKellar, Kopylov & Engel, 2013, but its placement in Labeninae is questionable (McKellar et al. 2013; Santos et al. in press).

In contrast to the Cretaceous, the Paleogene is dominated by extant ichneumonid subfamilies. Following a single ichneumonid from the Paleocene, *Phaenolobus arvenus* Piton, 1940, tentatively placed in Acaenitinae (Piton 1940), there is a rich ichneumonid fauna known from the Eocene and Oligocene. In total, 209 fossils species belonging to 19 extant and two fossil subfamilies were registered from this period (PaleoBioDB 2021), with the most significant deposits being the Florissant Formation and Green River Formation in the United States (Brues 1910; Spasojevic et al. 2018a), Aix-en-Provence in France (Theobald 1937), Rott Formation and Messel Pit in Germany

(Statz 1936; Spasojevic et al. 2018b), and Bembridge Marls from Bouldnor Formation in England (Cockerell 1921; Antropov et al. 2014). An early Eocene deposit, the Fur Formation in Denmark, also harbours numerous ichneumonid fossils (Rust 1998), although only a few have been described (Meier et al. 2022, Klopfstein 2021) and a large number remains unstudied. Although not many ichneumonids are known from Eocene and Oligocene amber deposits, some have been described from Baltic amber, which appears to have preserved a much higher diversity of ichneumonid subfamilies that previously thought (Manukyan and Zhindarev 2021). Banchinae, Cryptinae (sensu Townes 1970a), Diplazontinae (only through a puparium with an emergence hole typical for the subfamily), Hybrizontinae, Stilbopinae, Tryphoninae, Orthocentrinae and Pimplinae are all found in Baltic amber, as well as the extinct Townesitinae and Pherhombinae (Kasparyan 1988; Kasparyan 1994). Banchinae and Stilbopinae were also recorded in Rovno amber from Ukraine (Khalaim 2011). Although until now only a single ichneumonid has been described from early Eocene Oise amber, *Palaeometopius eocenicus* Menier et al., 2004 (Menier et al. 2004), it is an important deposit, as it provides more insights into the ichneumonid diversity close to the Cretaceous-Paleogene boundary.

Oise amber from several sites in the Paris Basin in France is a recently discovered deposit area from the early Eocene (Nel et al. 2004). It is dated back to the Ypressian, more precisely its sub-division Sparnacian (De Franceschi and De Ploëg 2003). In 1997 a new fossiliferous locality was discovered near the town of Creil and Houdancourt at the place known as 'Le Quesnoy' (Paris Basin, Oise, France) and dated to the lowermost Eocene, i.e., 55–53 Mya. This age was established by stratigraphy and confirmed by the presence of fossil remains of mammalian taxa, allowing a calibration against the mammalian layer reference. The amber was produced by angiosperms, most probably by *Aulacoxylon sparnacense* Combes, 1907 (Combretaceae or Caesalpiniaceae; De Franceschi and De Ploëg 2003). So far, many interesting inclusions have been found in this amber, ranging from different plant structures, feathers, hair, and coprolites from vertebrates, to a great diversity of insects. The composition of those fossils leads to the assumption of a subtropical environment, with a semi-deciduous or deciduous forest, and wet and dry seasons. In nearby sediments, fossils of amphibians and insect larvae that depend on aquatic habitats were found, suggesting a nearby freshwater source (Nel et al. 2004).

The preservation of some fossils in Oise amber, especially insects, is of high quality, with sometimes even internal soft tissues, like organs or musculature, clearly visible after the necessary scanning procedures (van de Kamp et al. 2014). It is in this respect comparable with Baltic amber (Grimaldi et al. 1994; Kehlmaier et al. 2014; Selden and Penney 2017). The insect diversity found in Oise amber was examined in 2009, and revealed about 17 insect orders with different family diversities (Brasero et al. 2009). While most orders are still poorly studied, others like the Psocoptera were examined rather well (Nel et al. 2005). The most diverse appear to be Coleoptera and Psocoptera, followed by Hymenoptera (Brasero et al. 2009). Within Hymenoptera eight families have been found so far, including both extant families of Ichneumonoidea; two species

of Braconidae have to date been described (Belokobylskij et al. 2010) and one species of Ichneumonidae (Menier et al. 2004).

We here conduct the first systematic study of Darwin wasps in Oise amber, based on the extensive collection of this amber at the Muséum Nationale d'Histoire Naturelle in Paris. We describe two new species and redescribe *Palaeometopius eocenicus*, while re-evaluating its subfamily placement. We find that all three examined fossils possess unique character combinations that require placing them in new genera. All three taxa combine plesiomorphic with derived character systems and are thus especially informative about character evolution in stem versus crown group Darwin wasps.

Materials and methods

All fossil specimens studied here come from the Oise amber deposit (49°20'06.0"N, 2°40'28.9"E). The amber pieces were first polished on one side to screen their content and then completely polished with a diamond disk to remove the weathered surface for optimal study of all inclusions. Then, the thin polishing marks on the amber surface were removed using diatomite. Amber fragments were immersed in water plus sugar solutions or in maple syrup to minimize light scattering during study and image capture (Sadowski 2021). Specimens were examined and photographed under a Nikon SMZ25 stereomicroscope with a Nikon D800 attached or with the Keyence VHX 600 system at magnification 200×. Some overview images were digitally stacked using photomicrographic composites of several individual focal planes, using HeliconFocus. The figures were composed with Adobe Illustrator CC 2019 and Adobe Photoshop CS19 software. All specimens are housed in the Palaeontological collection of the Muséum National d'Histoire Naturelle in Paris (**MNHN.F**).

We follow the open nomenclature framework (Matthews 1973) to express uncertainty in fossil classification. This framework uses question marks after the genus name to denote uncertain genus affiliation and expressions like "incertae familiae", "incertae sedis" and so on for higher-level classification. An uncertain subfamily placement would thus be indicated by "incertae subfamiliae" (e.g., Spasojevic et al. 2018a, 2018b). This can be very useful if subfamily affiliation is indeed mostly unknown or if only a handful of subfamilies exist within a family. However, as Ichneumonidae consists of 42 extant and six extinct subfamilies, we deem it important to also be able to express an uncertain placement within one particular subfamily, for instance in cases when all characters seen in a fossil are consistent with such a placement, but the unique synapomorphies of the group are not visible. We simply extend the framework by adding a question mark after the subfamily name in such cases.

Morphological terminology follows Broad et al. (2018), except for the wing terminology, which follows Spasojevic et al. (2018a). Tergites and sternites are often numbered in the text and abbreviated as "T1", "T2", etc. and "S1", "S2" etc., respectively. Measurements were either taken directly from the fossils using an eyepiece with a scale or measured in ImageJ (Schneider et al. 2012) from photographs made without stacking. Unless stated otherwise, measurements correspond to lengths of the

respective structures. In those cases where photographs were deemed insufficient to illustrate our analyses of the fossils, interpretative drawings were made as overlaid layers in Adobe Photoshop (v. 21.2.3).

Results

We examined more than 1,000 pieces of amber from Oise in search of Ichneumonidae, but only found two nearly complete specimens. In contrast, there were more than 60 amber pieces with Braconidae recovered, several dozen Aculeata (mostly Crabronidae), many Formicidae, and numerous Chalcidoidea and other small-bodied Hymenoptera. In Braconidae, a large proportion of the specimens could be identified as belonging to Cheloninae, a subfamily with representatives with a body size of about 4–6 mm, which is rather large for a braconid and comparable to many ichneumonids.

Along with the newly found specimens, we examined and redescribed the holotype of *Palaeometopius eocenicus*, which until now was the only ichneumonid found in Oise amber. The other two represent new species and will be described below.

Systematic palaeontology

Hymenoptera Linnaeus, 1758
Ichneumonidae Latreille, 1802
Tryphoninae? Förster, 1869

***Palaeometopius eocenicus* Menier et al., 2004**
Figs 1, 2

Systematic placement. Menier et al. (2004) placed their monotypic genus in Metopiinae, stating that it "shares the main diagnostic characters of the Metopiinae, as defined by Townes (1971)". Examining the holotype at MNHN.F, we found the evidence for such a placement unconvincing. This has already been indicated by the list of characters mentioned by the original authors as differing between the fossil and all other Metopiinae. In fact, this subfamily is one of the very few among Ichneumonidae that has a unique character to define it: the upper margin of the face is extended as a triangular process between the antennal sockets. While Menier et al. (2004) mentioned that his process was shorter in the fossil than in the extant species of the subfamily, we could not find any trace of it. Several other characters disagree with a placement in Metopiinae, including the long notauli that meet medially on the mesoscutum in the fossil; the strongly inclivous vein 2m-cu in the forewing with two widely separated bullae; and finally, the rather long ovipositor.

In contrast, all the characters visible in the fossil are in accordance with a placement in Tryphoninae, especially the strong and complete propodeal carination, the broad first tergite, the strongly convergent notauli, and the stout ovipositor, lacking a distinct

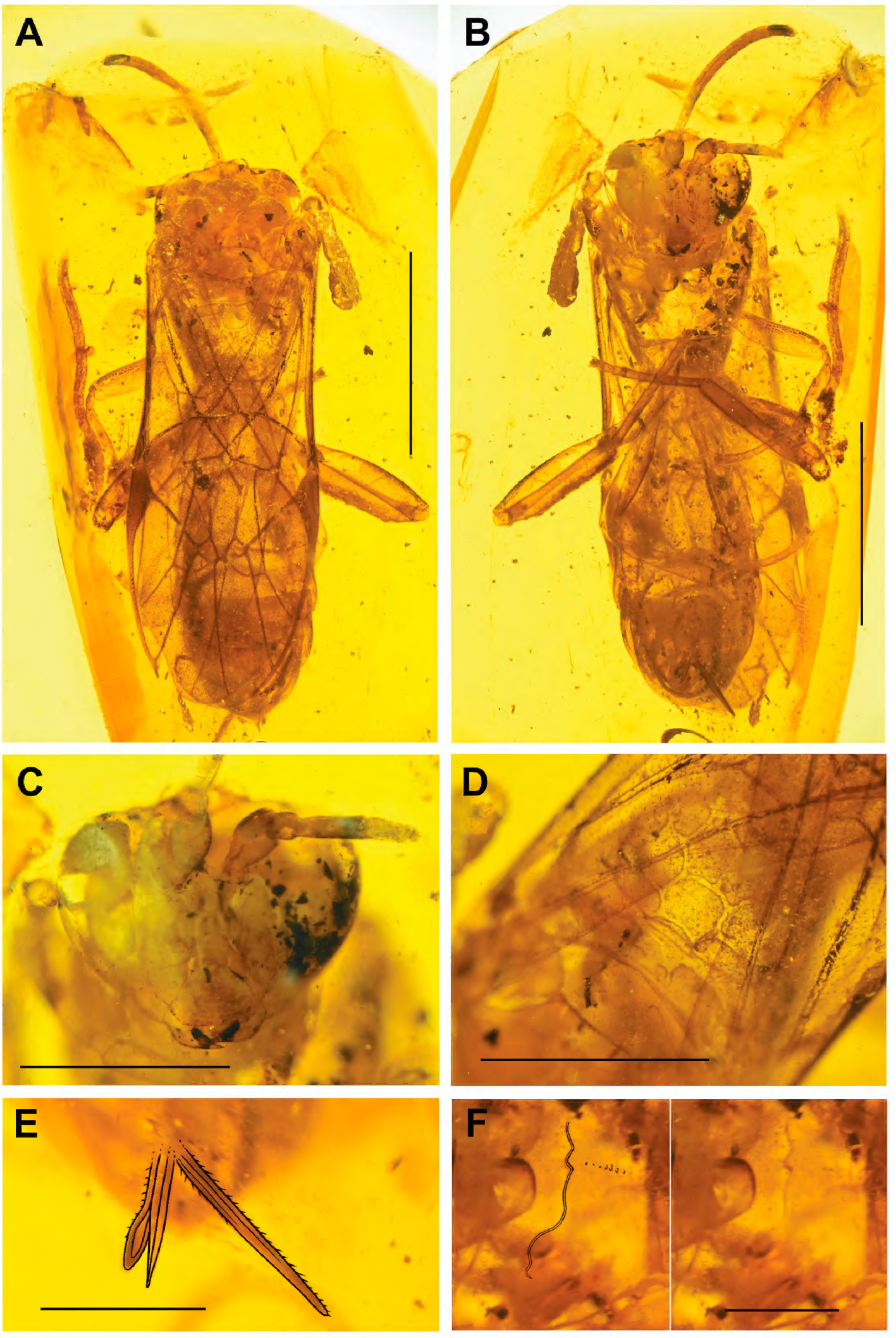

Figure 1. Holotype of *Palaeometopius eocenicus* Menier et al., 2004 **A** dorsal view of whole specimen **B** ventral view of whole specimen **C** front view of face **D** dorsal view of propodeum **E** ovipositor and ovipositor sheaths **F** epicnemial carina on ventral side. Scale bars: 2 mm (**A, B**); 1 mm (**C, D**); 0.5 mm (**E, F**).

nodus or dorsal subapical notch. Also, none of the characters in the fossil are entirely absent from extant Tryphoninae, although some, such as the twisted mandibles and the clearly protruding ovipositor, are rather rare (other than in *Netelia* Gray, 1860. However, the combination of characters shown in the fossil is not in accordance with any of the extant tribes (Bennett 2015). There are two apomorphic characters uniting extant Tryphoninae, the stalked egg, which is often carried exposed on the ovipositor, and a fringe of long, parallel setae on the clypeus. Neither are visible in the fossil, either due to absence or just preservation or poor visibility. We thus label our placement of this fossil in Tryphoninae as tentative.

Material examined. France • ***Holotype*** female; Oise department, region of Creil, Chevrière, Le Quesnoy; 49°20'06.0"N, 2°40'28.9"E; G. De Ploëg leg.; in amber mounted in Canada balsam; MNHN.F.A30079 (PA2439).

Type condition. Nearly complete specimen; apical part of right and median part of left antenna, right foreleg from tibia and apex of left fore tibia missing; wings folded over metasoma, obscuring view on tergites; milky substance present ventrally from metasoma, thus in part obscuring view on sternites. Cuticula translucent in most places, interior partly hollow, organs partly preserved.

Description. Body 5.6 mm. Colour or colour pattern not visible.

Head. Mandibles long and overlapping, curved along main axis and strongly twisted; bidentate, with lower tooth about half as long as upper one. Labrum concealed below clypeus. Clypeus somewhat convex in profile, probably weakly separated from face; apical margin truncate medially, curved upwards laterally. Malar space clearly longer than mandibular width at base. Anterior tentorial pits distinct. Shape of face difficult to discern, but probably rather flat with weak median swelling. Eyes in profile about 0.8× height of head. Upper margin of face without process, without modification between antennal sockets. Frons without strong impressions for scape. Ocelli of normal size. Maxillary palp with five segments, labial palp not entirely visible. Scape slightly longer than wide; truncation strongly oblique, forming an angle of about 45° with the main axis. Pedicel much shorter and smaller than scape. Antenna 4.2 mm, with 25 flagellomeres, evenly thick throughout entire length; first flagellomere 3.2×, subapical flagellomere 1.1× as long as wide.

Mesosoma. Pronotum rather short, well visible around front half of mesoscutum when viewed from above; without modification at base of notaulus; with at least dorsal part of epomia present. Mesosternum with deep scrobe with cross-carinulae; posterior transverse carina absent. Sternaulus deeply impressed anteriorly, seemingly reaching only to about 0.4× length of mesopleuron. Epicnemial carina complete ventrally, dipped in mesosternal scrobe; laterally forming two widely spaced, strong curves; upper end not discernible. Mesopleuron only visible at angle, rather short; with short impression at around mid-height in front, where epicnemial carina shows a second curve above the one accommodating the sternaulus; mesopleural furrow not discernible. Notauli deeply impressed, with some cross-carinulae in the impression; strongly converging, meeting in an impressed area medially on mesoscutum. Scutellum short and wide, without lateral carinae; metanotum of normal length and convex. Submetapleural

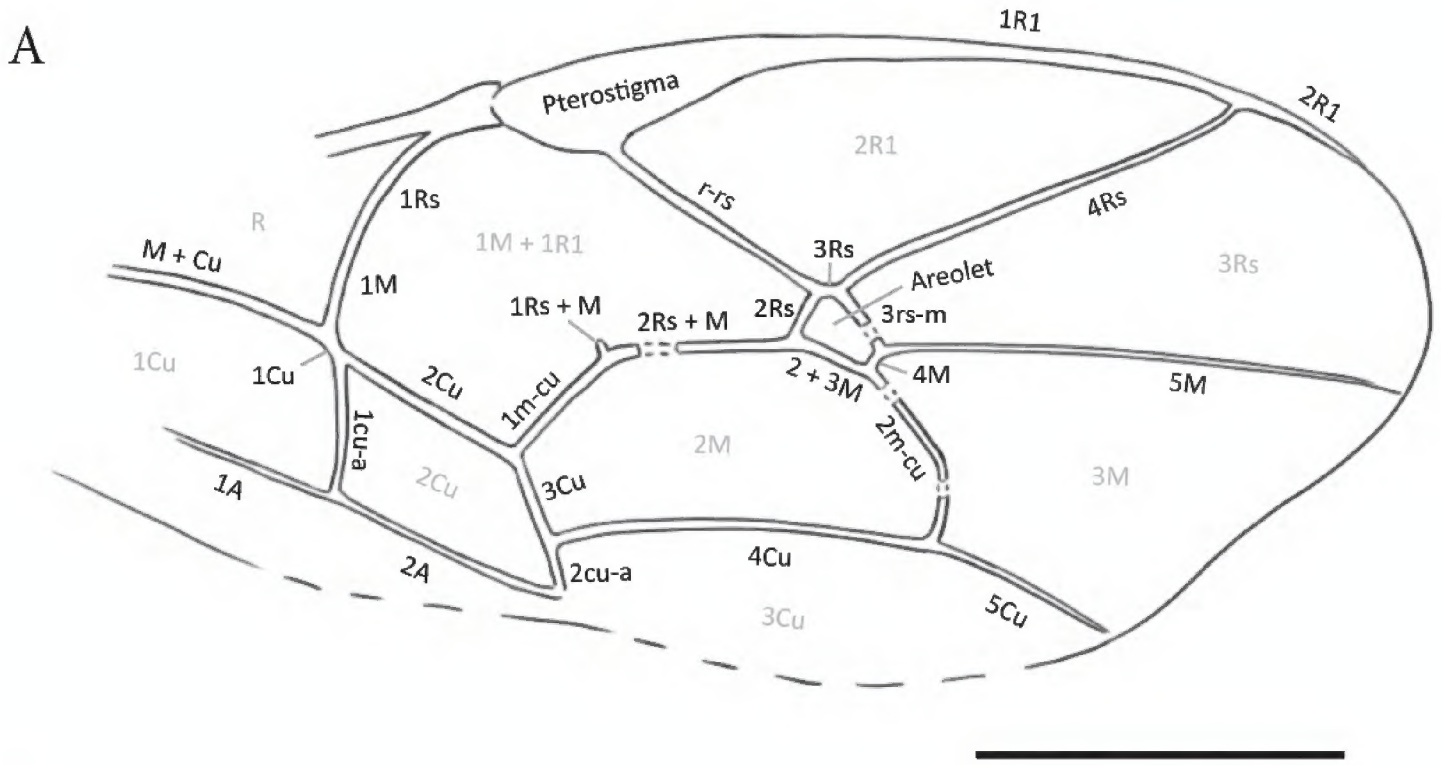

Figure 2. Interpretative line drawings of the wings of *Palaeometopius eocenicus* Menier et al., 2004 with venation nomenclature in black and cell nomenclature in grey **A** fore wing **B** hind wing. Scale bar: 1 mm (**A, B**).

carina complete, pleural carina not visible. Propodeum in profile somewhat shortened; carination complete, with latero-median- and lateral longitudinal carinae, anterior and posterior transverse carinae; all carinae strongly angled at meeting points; area basalis very much shortened, area superomedia wider than long, area petiolaris with an additional median longitudinal carina nearly as strong as remaining carinae. Hind margin of propodeum simple. Legs simple, coxae simply convex; fore tibia simple to slightly enlarged, mid and hind tibiae with two spurs; hind coxa evenly rounded, a little longer than wide. Hind tarsomeres deeply excised on dorsal side. Claws short and stout, simple, arolium shorter than claws.

Wings. Fore wing 4.8 mm. Areolet closed, pentagonal-oblique, 3rs-m with one bulla, about as long as 2 + 3M, 4M very short. 2m-cu inclivous and strongly bowed outwards, with two small, about evenly spaced bullae. 4Cu nearly twice as long as 5Cu. 4Rs straight. 1Rs + M about as long as width of surrounding veins. 1cu-a at junction of M

+ Cu and 1M or nearly so. Pterostigma 4.0×, cell 2R1 2.5× as long as wide. 5M entirely tubular. 2Cu 0.8× of 1M + 1Rs, 0.85× of r-rs. 1m-cu & 2Rs + M angled. 3Cu clearly longer than 2cu-a. Hind wing with M + Cu complete, slightly curved on entire length. 1Cu about 0.6× cu-a. 1Rs about 1.5× rs-m, although upper end hardly discernible.

Metasoma. Sternites poorly visible, weakly sclerotized; hypopygium short, transverse, appears weakly sclerotized. T1–T4 depressed, apex of metasoma about circular. T1 poorly visible, appears subquadrate, evenly tapering anteriorly in dorsal view; spiracle seems around middle; latero-median carina seems present, widely parallel. T2 transverse, appears normally separated from T3. T4 and T5 well developed; T6 and following tergites very short and hidden below anterior tergites. T8 short, not elongated in horn or boss. Ovipositor sheaths about 0.7 mm, evenly setose, parallel, then tapering from about mid length. Ovipositor tip region rather long, evenly tapering, without discernible teeth.

Tryphoninae? Förster, 1869

Pappous gen. nov. (masculine)

http://zoobank.org/ED549916-A111-4353-A55D-3DEAD7A0A980

Etymology. Derived from the Greek word (*pappoús*) for grandfather, which highlights the age of the genus.

Type species. *Pappous trichomatius* sp. nov.

Systematic placement. The most conspicuous character of this fossil is probably the dense pilosity on the compound eyes, which is rather rare in Ichneumonidae. However, there are a few genera or species with setose eyes in a large portion of the subfamilies (*Schizopyga* Gravenhorst, 1829 and *Dreisbachia* Townes, 1962 in Pimplinae; *Trichomma* Wesmael, 1849 and *Ophionellus* Westwood, 1874 in Anomaloninae, *Cymodusa* Holmgren, 1859 in Campopleginae, *Collyria trichophthalma* Thomson, 1877 in Collyriinae, etc.) (Townes 1969, 1970b, 1971).

The fossil shares some similarities with taxa in the subfamily Orthocentrinae. First, the face of the fossil reminds of taxa in the *Helictes* genus-group, with a strongly convex clypeus both in front and profile view, a rather long malar space and tentorial pits that are placed much behind the clypeal plane (Townes 1971). Second, the converging but almost box-like first tergite with the spiracle around the middle, and strong and parallel latero-median carinae also occur in Orthocentrinae. Third, there are also some *Eusterinx*, in the subgenus *Trestis*, that share the setose eyes. All Orthocentrinae possess a conspicuous fringe of setae along the inner side of the hind tibia, but this body part is unfortunately not visible. However, the relatively short and fully carinated propodeum speak against most Orthocentrinae, except *Eusterinx*, and the mentioned characteristics also appear in some Tryphoninae taxa, and since many characters in Orthocentrinae are very variable and seem plesiomorphic in the fossil, a placement in Orthocentrinae seems ill-advised.

Altough the setose eyes are a highly homoplastic character, it might give an important hint, as eyes with conspicuous setae occur rather often in Tryphoninae (e.g., *Thymaris* Förtster, 1869, *Oedemopsis* Tscheck, 1869, *Zagryphus* Cushman, 1919), in the tribe Oedemopsini (Bennett 2015). Indeed, the combination of characteristics in this fossil are all consistent with a placement in Tryphoninae. The setose eyes and strongly tapered mandibles, the deeply impressed notauli, together with the full carination on the propodeum, lead to some genera in the tryphonine tribe Oedemopsini (Bennet 2015; Broad et al. 2018). The mesosoma, the very strong juxtacoxal carina, the posterior transverse carina of the mesosternum, which forms a lobe with the lateral part and is medially expanded into two lobes, as well as the shape of the first tergite are rather similar to *Acaenitellus* Morley, 1913. The setose eyes and mandible shape on the other hand would point to a close resemblance to *Thymaris* and *Neliopisthus* Thomson, 1883. The latter also shares similarities in the first tergite, which is in some species tapered gradually with more or less parallel latero-median carina. But although the fossil shares many characteristics that are consistent within Oedemopsini, it also features differences, which are rare in this tribe: a strongly bowed 2m-cu, a rather stout and box-like first tergite, and a closed areolet. The latter is only present in *Leptixys* Townes, 1969 from Chile and Argentina, *Debophanes* Gauld, 1984 from Australia and the fossil species *Thymariodes areolaris* Kasparyan, 1988 from Baltic amber (Bennet 2015). Although we have good arguments forplacing *P. trichomatius* in Oedemopsini, important characteristics, like an antenna with a median light-coloured band, simple tarsal claws and an ovipositor with a weakly sclerotized ventral valve (Bennet 2015), which would distinguish this tribe from other Tryphoninae, are not visible. Therefore, we do not place the fossil in this tribe or any Tryphoninae tribe. Since the previously mentioned apomorphic characters in extant Tryphoninae, the stalked egg and the fringe of setae on the clypeus, are not visible in this fossil, we also label our placement of this fossil in Tryphoninae as tentative.

Diagnosis. *Pappous* gen. nov. differs from the only known fossil genus of Oedemopsini, *Thymariodes* Kasparyan, 1988, described from Baltic amber, in having unidentate or strongly twisted mandibles, a convex clypeus in profile, a longer malar space, as well as a long and slender pterostigma, an outwards bowed 2m-cu and with vein 1Rs + M present. It also differs from *Palaeometopius* by the shape and dimension of the mandibles, the presence of conspicuous setae on the eyes, and a quadrate-oblique areolet shape. In addition, *Pappous* gen. nov. differs from extant genera in Oedemopsini by its closed quadrate-oblique areolet, a strongly carinated propodeum, and subquadrate and non-petiolate T1. Since *Pappous* does have a different character combination than extant Oedemopsini or other Tryphoninae genera, we propose a new genus.

The genus combines dense and conspicuous setae on the eyes, a convex clypeus with simple margin, the malar space about as long as base width of mandibles or a little longer, a weak oblique truncation of the scape, a strongly areolated propodeum with rather simple surface sculpture and complete juxtacoxal carinae, fore wing with closed quadrate-oblique areolet and a box-like first tergite.

***Pappous trichomatius* sp. nov.**
http://zoobank.org/A6ACD113-6520-40E8-91EF-3FD2678B05FD
Figs 3, 4

Etymology. A combination of the two Greek words trichotos (hairy) and matius (matia for eyes), describing the short but regularly spaced setae on the fossil's eyes.

Material examined. France • ***Holotype*** male?; Oise department, region of Creil, Chevrière, Le Quesnoy; 49°20'06.0"N, 2°40'28.9"E; 1998–2000; G. De Ploëg and A. Nel leg.; in amber; MNHN.F.A71346 (PA-349).

Type condition. Fossil not complete and partially hidden by an insect inclusion, probably a Trichoptera. Head complete, but partially hidden behind other inclusion. Pronotum and metapleuron partially hidden by wings. Mesoscutum, scutellum and metanotum broken off. Propodeum and T1 well preserved. Legs mostly hidden. Dorsally broken after T2, ventrally after S6, but otherwise well preserved. Lateral view of T1–T4 partially visible on one side.

Diagnosis. See genus diagnosis.

Description. Body at least 5.6 mm (measured from head to T1, added length of T2-T5 in segments), estimated length about 6.1 mm. Colour and colour patterns not interpretable, because of dark orange colour of amber.

Head. Mandibles rather long and overlapping; seem unidentate or second tooth twisted and mandibles bidentate; outer surface sparsely pubescent. Malar space about 0.9–1.2× mandibular width. Labrum concealed below clypeus. Clypeus convex, weakly separated from face; apical margin simple. Anterior tentorial pits distinct. Face rather flat with weak median swelling. Eyes in profile about 0.8× height of head, with short but dense setae. Modifications between antennal sockets unclear. Frons without impressions. Ocelli of normal size, separated from eyes by more than their diameter. Vertex seems moderately long and rather flat. Occipital carina seems complete. Palps not visible. Scape longer than wide; truncation rather straight, forming an angle of 10°; without extended membranous area. Pedicle smaller than scape. Flagellum 4 mm long, with 23 segments, evenly thick throughout whole length; most flagellomeres about 1.5× as long as wide; first flagellomere 2.9× as long as wide; tip of last flagellomere unmodified.

Mesosoma. Propleuron not visible. Pronotum about 0.6–0.7× as long as high; epomia indiscernible; without modification at base of notaulus. Mesosternum with epicnemial carina partially visible ventrally, seems simple behind fore coxae; posterior transverse carina of mesosternum not discernible. Small lobe in lower hind corner of mesopleuron with two short extensions; mesopleuron rather short and flat, with sternaulus anteriorly visible, appears weak. Mesoscutum mostly broken off, difficult to interpret, with notauli deeply impressed. Scutellum not visible and metanotum rather short and flat. Metapleuron seems slightly higher than long or just about as long as high. Submetapleural carina complete with a small lobe on anterior part. Juxtacoxal carina very strong. Pleural carina distinct on whole length. Propodeum in profile seems evenly rounded and slightly shorter than high or similar in length as in height; sculpture seems smooth with very weak rugae occasionally; carination complete, with

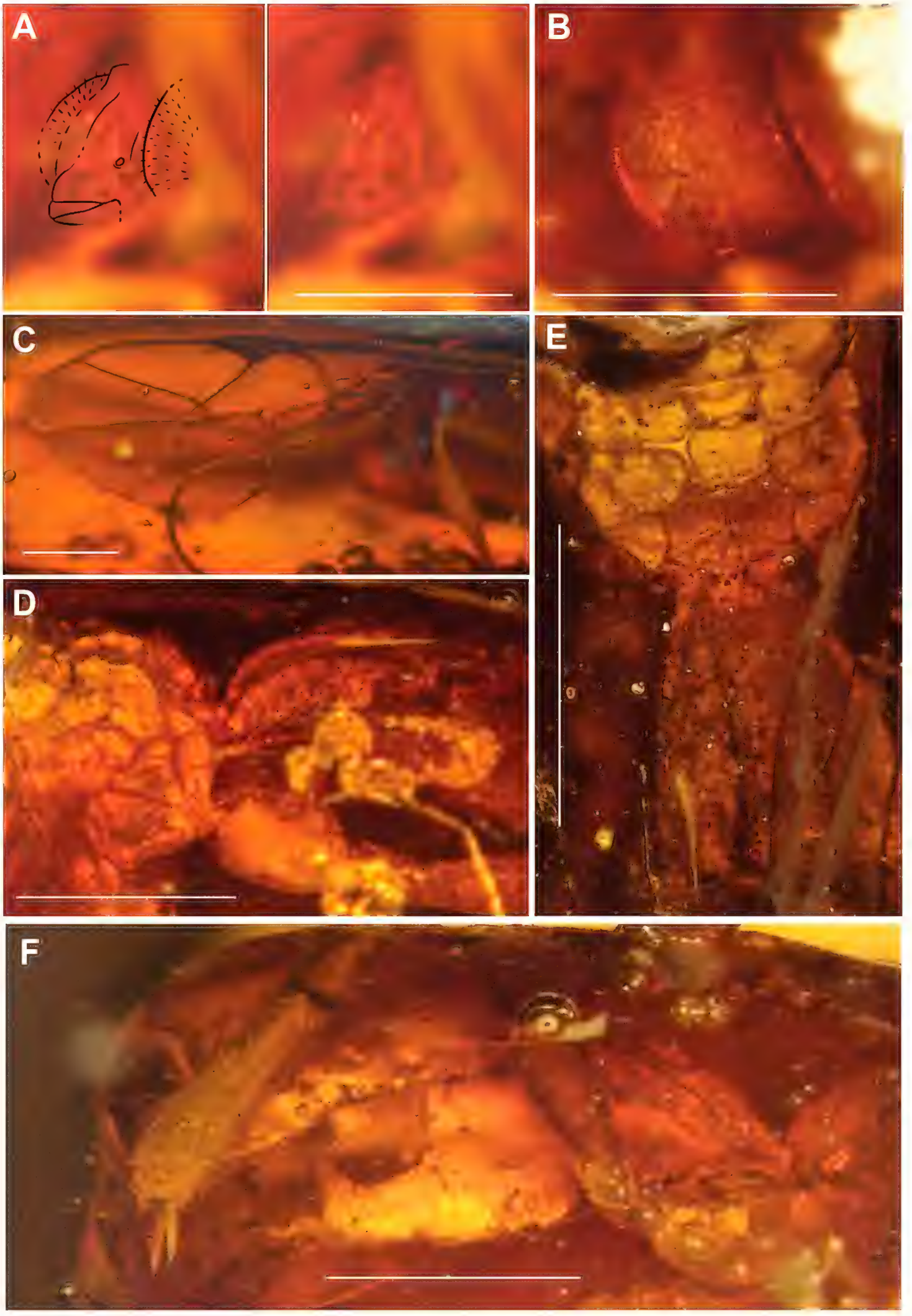

Figure 3. Holotype of *Pappous trichomatius* sp. nov. **A** latero-ventral view of face with and without interpretative drawing **B** lateral view of eye with short and dense setae **C** fore wing **D** lateral view on propodeum and first tergite **E** dorsal view on propodeum and first tergite. Scale bars: 1 mm.

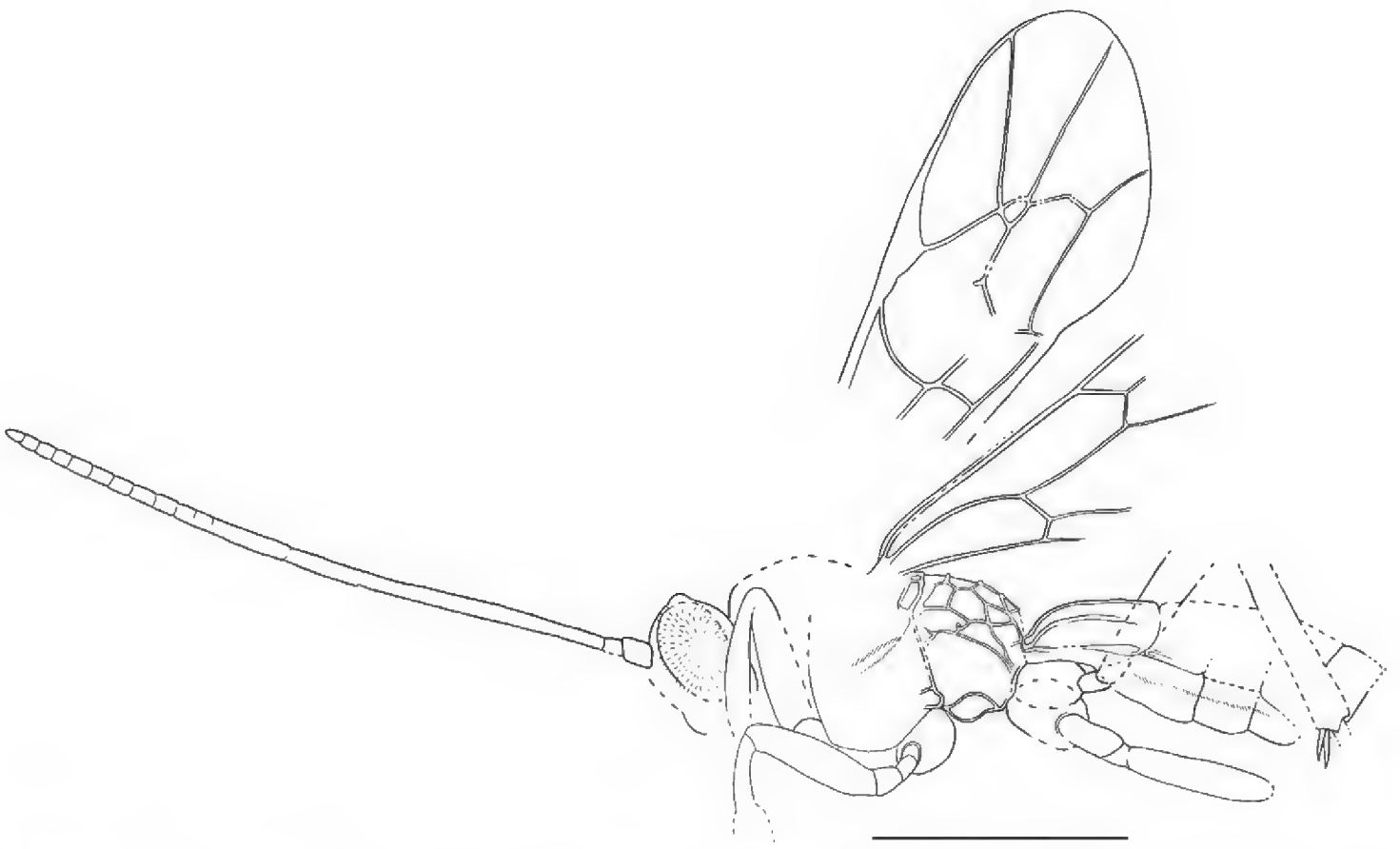

Figure 4. Interpretative line drawing of *Pappous trichomatius* sp. nov. Dotted lines indicate uncertain interpretations. Photographs from different angles were used as templates to create a drawing of the whole specimen. Scale bar: 2 mm.

latero-median and lateral longitudinal, anterior and posterior transverse carinae present, latter two carinae angled; area superomedia wider than long, area petiolaris with an additional median longitudinal carina. Posterolateral angle evenly rounded. No modifications on junctions of propodeal carinae or surface. Spiracle subcircular. Hind margin of propodeum simple. Metacoxal cavity seems to begin slightly above ventral end of metasomal foramen magnum. Legs simple, fore tibia seems simple to slightly enlarged, with two spurs. Mid coxa simply convex, mid tibia with two spurs. Hind coxa evenly rounded, seems as long as wide. Hind femur and tibia simple, tibia evenly tapered. Inner side of hind tibia not visible. Claws indiscernible.

Wings. Fore wing 5.4 mm. Areolet closed, quadrate-oblique, 3rs-m with one bulla and same length as 2 + 3M, 4M extremely short. 2m-cu more or less evenly bowed outwards with two small bullae that cover together ~25% of total 2m-cu length. 4Cu about twice as long as 5Cu. 4Rs almost straight. Vein 1Rs + M about 1.5–2× longer than with of surrounding veins. 1cu-a posterior to junction of M + Cu and 1M, with 1Cu as long as width of surrounding veins. Pterostigma 3.0× as long as wide. Cell 2R1 2.9× as long as wide. 5M tubular through whole length. 2Cu 0.7× 1M + 1Rs and 0.8× r-rs. 1m-cu & 2Rs + M angled. 3Cu slightly longer than 2cu-a. Hind wing with M + Cu complete, slightly curved on entire length. 1Cu about 0.6× cu-a. 1Rs about 1.4× rs-m.

Metasoma. Appears depressed, after T4 unclear. S1 seems either not ornamented or with a low rounded swelling and hind margin transverse to shallowly V-shaped. Apical fusion of S1 to T1 is unclear. Laterotergite 1 short and triangular, at least partly sclerotized. Glymma seems absent or weakly impressed. T1 subquadrate, evenly

tapering to front in dorsal view; rather flat with weak median curve in profile; dorsal sculpture seems either smooth and impunctate or finely punctate. Dorso-lateral carina of T1 complete, above spiracle. Spiracle at around 0.6× of T1. Latero-median carina of T1 parallel, reaching beyond middle of total length. T2 is transverse without latero-median carinae, appears simple, with shallow impression close to base; thyridium present but not sunken in gastrocoelus, seems either ovoid or transverse. Laterotergite 2 moderately broad, sclerotized, and between 0.25–0.4× as wide as long, seems to have a shallow groove from base to spiracle. T2 and T3 separate. Laterotergites 3 and 4 appear separated by a crease.

Phygadeuontinae Förster, 1869

Madma gen. nov. (feminine)

http://zoobank.org/C7D5C3FD-1E5C-4D8A-859A-A232EB122A1C

Etymology. The genus name comes from the French word "Mademoiselle", which means "Miss". "Madma" is also a Filipino word for "Madam". The word is chosen to create a wordplay together with the name of the type species (see below).

Type species. *Madma oisella* sp. nov.

Systematic placement. The presence of a sternaulus, a pentagonal areolet, and the outwards bowed 2m-cu with two bullae, reminds of Claseinae at first. But in Claseinae the sternaulus is not reaching to the posterior end of the mesopleuron, the carination on the propodeum is largely reduced, the areolet smaller and the ovipositor is rather long, which makes this subfamily unlikely. Several characters associate this fossil with crown Phygadeuontinae: the petiolate T1 with the spiracle behind the middle; the long sternaulus that reaches the posterior margin of the mesopleuron above mid-height of the mid coxa; the short ovipositor with a nodus on the dorsal and oblique teeth on the ventral valve; and the two bullae in fore wing vein 2m-cu (Townes 1970a; Santos 2017). However, the wide and unevenly pentagonal areolet with 4M significantly shorter than 2 + 3M, and the presence of a tooth on the apical margin of the fore tibia, do not occur in extant phygadeuontines. The tooth on the fore tibia is a homoplastic character occurring in multiple subfamilies across the ichneumonid tree, including Tryphoninae, Ctenopelmatinae, Tersilochinae, Metopiinae, Anomaloninae, Campopleginae and the more distantly related Eucerotinae and Labeninae (Townes 1969, 1970a, 1970b, 1971); it is thus not informative for the subfamily placement. The wide, pentagonal areolet is a rather plesiomorphic character which only occurs in the Cretaceous Labenopimplinae (Kopylov 2010b) and in extant and fossil Labeninae (Townes 1969; McKellar et al. 2013; Spasojevic et al. 2018b), including a tentative labenine from Cretaceous Canadian amber (McKeller et al. 2013), *Albertocryptus dossenus*. *Madma* clearly differs from Labenopimplinae and Labeninae based on the shape and position of T1 relative to the metacoxal cavities, but resembles *A. dossenus* in both areolet shape, two bullae in 2m-cu and the petiolate T1; it differs from it in the number of flagellomeres (17 in *A. dossenus*) and the much stouter scape, T1 and hind coxae. The wide pentagonal areolet, together with other plesiomorphic characters,

such as two bullae in 2m-cu and a long, strong carinae on T1 and long ovipositor, suggest *Madma* being a stem lineage of Phygadeuontinae or, less likely, its position further down the Ichneumoniformes tree. Given that Phygadeuontinae are currently polyphyletic (Santos 2017), we in fact also cover the latter scenario when placing the fossil in Phygadeuontinae; once Phygadeuontinae are revised in the light of further phylogenetic evidence, this placement will have to be reviewed.

Diagnosis. *Madma* gen. nov. differs from all other Phygadeuontinae genera in having a bilobed posterior transverse carina on the mesosternum, a tooth on the apical margin of the fore tibia and an unevenly pentagonal areolet with 4M shorter than 2 + 3M. In addition, the genus is characterised by the following characters: 2m-cu curved outwards, with two bullae; mesopleuron with complete sternaulus curved around middle, reaching posterior margin of mesopleuron above mid-height of mid coxa; T1 petiolate with parallel and long latero-median carinae almost reaching its posterior margin; ovipositor slightly longer than height of metasoma at apex, straight and its apex with a nodus on upper valve and oblique teeth on lower valve.

***Madma oisella* sp. nov.**

http://zoobank.org/83D47279-D75A-4BEB-80E9-9F3BA89F0A30

Figs 5, 6

Etymology. Derived from the locality name: Oise. The word is transformed to resemble the ending of the French word for Miss "Madmoiselle" and latinised.

Material examined. France • ***Holotype*** female; Oise department, region of Creil, Chevrière, Le Quesnoy; 49°20'06.0"N, 2°40'28.9"E; 1998–2000; G. De Ploëg and A. Nel leg.; in amber; MNHN.F.A71347 (PA2189).

Type condition. Lateral aspects clearly visible through amber; dorsal and ventral aspects partly visible through irregular surface of amber. Complete, except few apical flagellomeres at surface of amber with their ventral side missing. Body translucent, thus parts of body from opposite side often visible below cuticle, as well as some inner structures. Body surface sculpture and carinae weakly visible; outer surface partly covered with dark material, which probably represents remains of organic matter.

Diagnosis. See genus diagnosis.

Description. Body around 4.9 mm. Color difficult to interpret, except tip of mandibles darker, hind tibiae clearly darker at base and apex (dark-light-dark), antennae uniformly colored and T1 dark.

Head. Mandibles moderately large, weakly tapered from base to apex, not twisted, with two oblique and subequal teeth; outer surface without strong sculpture, smooth or sparsely pubescent. Malar space moderately long, 0.9× mandibular width at base, smooth, seemingly without subocular sulcus. Labrum not clearly exposed below clypeus. Clypeus in frontal view subquadrate, transversely undivided and separated from face with weak clypeal groove, in lateral view clearly convex; apical margin simple, truncate, without tooth or tubercles. Face weakly convex with weak median swelling, without upper process. Eyes large, in lateral view 0.85× head height; inner margin of eyes

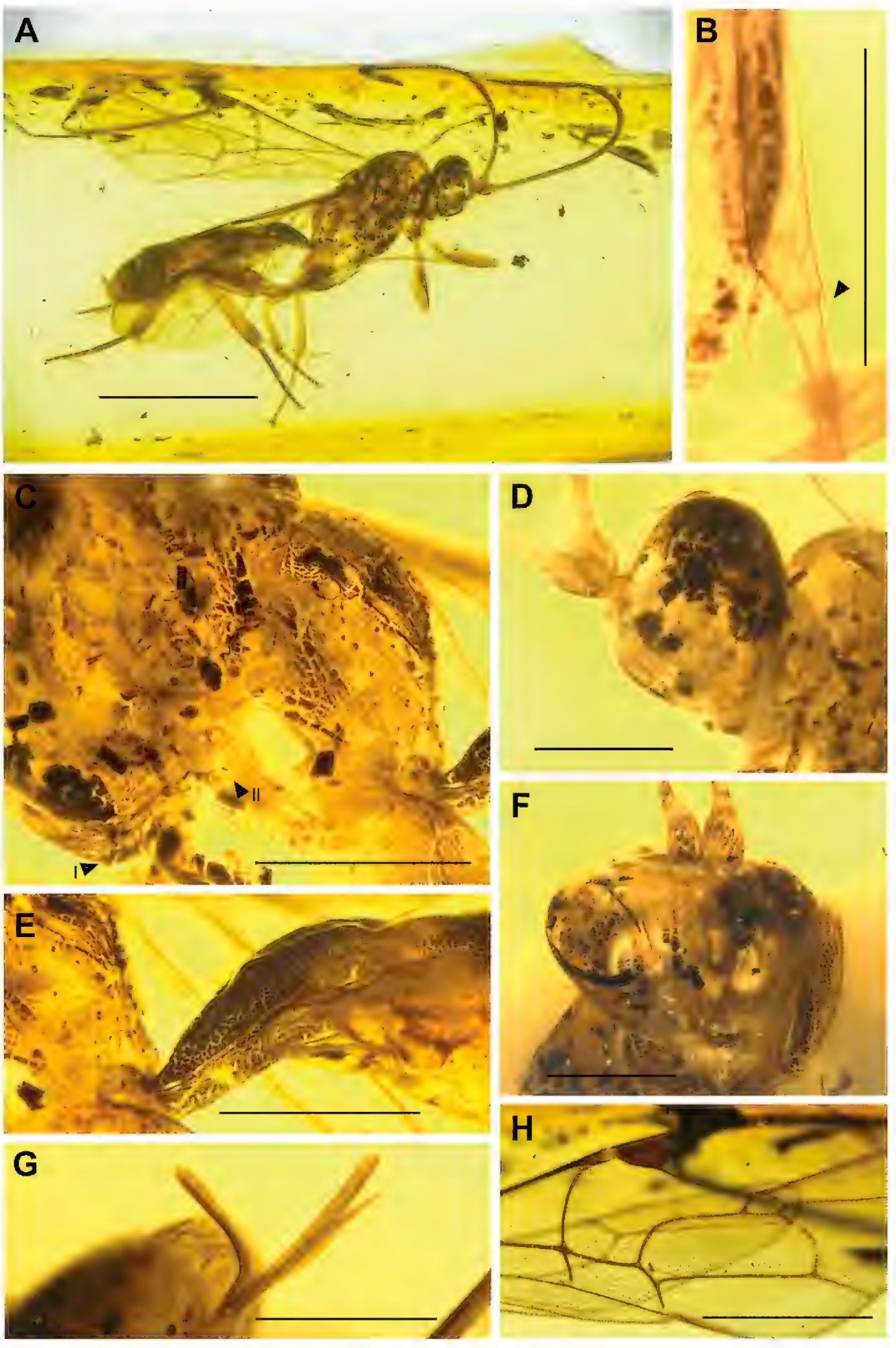

Figure 5. Holotype of *Madma oisella* sp. nov. **A** lateral view of whole specimen **B** fore tibia, black triangle points to tooth on apical margin **C** latero-ventral view showing propodeum and bilobed posterior transverse carina on mesosternum (I) and extended small lobe on metapleuron (II) **D** lateral view of head **E** first tergite and sternite **F** frontal view of face **G** ovipositor **H** Detailed photo of fore wing. Scale bar: 2 mm (**A**); 0.5 mm (**B, D–G**); 1 mm (**H**).

straight opposite antennal sockets, in frontal view parallel to each other. Modification between antennal sockets absent. Frons without strong impressions for scape. Ocelli of normal size, separated from eyes by more than their diameter. Vertex steeply declivous behind ocelli with straight surface to occipital carina. Occipital carina complete and dorsally evenly convex, high on head, in lateral view almost reaching height of dorsal eye margin. Maxillary palps with five segments, labial palps not visible. Scape about as long as wide, without extended membranous area; pedicel clearly smaller than scape. Flagellum 3.9 mm with 27 segments; first flagellomere 6.25× as long as wide; median and apical flagellomeres longer than wide; tip of apical flagellomere unmodified.

Mesosoma. Pronotum in profile on left side higher than long, on right side about as high as long (specimen clearly viewed only in slight diagonal position), without latero-ventral posteriorly projecting lobe; pronotal collar not visible; anterior vertical part clearly extended dorsally. Epomia weakly visible, present ventrally, extending laterally but unclear how far. Modifications near base of notauli absent. Mesosternum with epicnemial carina extending laterally on mesopleuron at least to mid-height of pronotum, possibly longer, but dorsal part not visible clearly through amber; not modified behind fore coxae. Posterior transverse carina absent laterally, present in front of mid coxae as a raised flange and in between as a low carina. Mesopleuron evenly convex with sternaulus weakly visible, extending from ventrolateral anterior margin of mesopleuron to posterior margin of mesopleuron clearly above mid-height of mid coxa, bowed upwards around mid-height. Mesopleural furrow with horizontal impression extending from around mid-height to episternal scrobe. Mesoscutum evenly shagreened and matt. Notauli deeply impressed anteriorly, extending posteriorly past centre of mesoscutum but unclear how far. Carina along lateral margin of mesoscutum evenly raised and extending to anterior margin of scutellum. Scutellum in profile flat, smooth, without carinae. Postscutellum evenly convex in profile. Propodeum about as long as high; structure difficult to assess but either smooth or punctured. Metapleuron as long as high, with anteroventral corner extended to a small lobe, without juxtacoxal carina and at most with few rugae lateroventrally. Submetapleural carina difficult to interpret, present only in anterior half or completely absent. Propodeal carination complete, although presence of medial portion of anterior transverse carina uncertain; area basalis shorter than area superomedia; the latter similar in size to area petiolaris. Spiracle subcircular, separated from pleural carina by its own diameter, touching dorsal half of pleural portion of lateral longitudinal carina. Dorsal margin of metacoxal cavities above ventral margin of metasomal cavity. Legs simple, not unusually stout or slender. Fore tibia with small apical tooth. Mid and hind tibia with two long slender spurs. Hind tibia with fringe of parallel setae on inner apex; 1st tarsomere 1.1× as long as wide; 4th tarsomere apically more or less evenly truncated. Tarsal claws without modification.

Wings. Fore wing 3.8 mm. Areolet oblique pentagonal, 1.5–2.2× as wide as long, with 3Rs 0.8× 2Rs, 2 + 3M 2.1× 2Rs, 4M 0.3× 2 + 3M; 3rs-m with two bullae. 2m-cu clearly curved outwards, with two bullae. 1Rs + M absent. 1m-cu at level of 1M + 1Rs. Pterostigma 4.3× as long as wide. Cell 2R1 2.1× as long as pterostigma, 3.4× as long as wide. 2Cu 0.8× 1M + 1Rs, 0.8× r-rs. 3Cu about same length as 2cu-a. Hind wing with M + Cu curved distally. 1Cu around same length as cu-a. 1Rs 1.2× as long as rs-m.

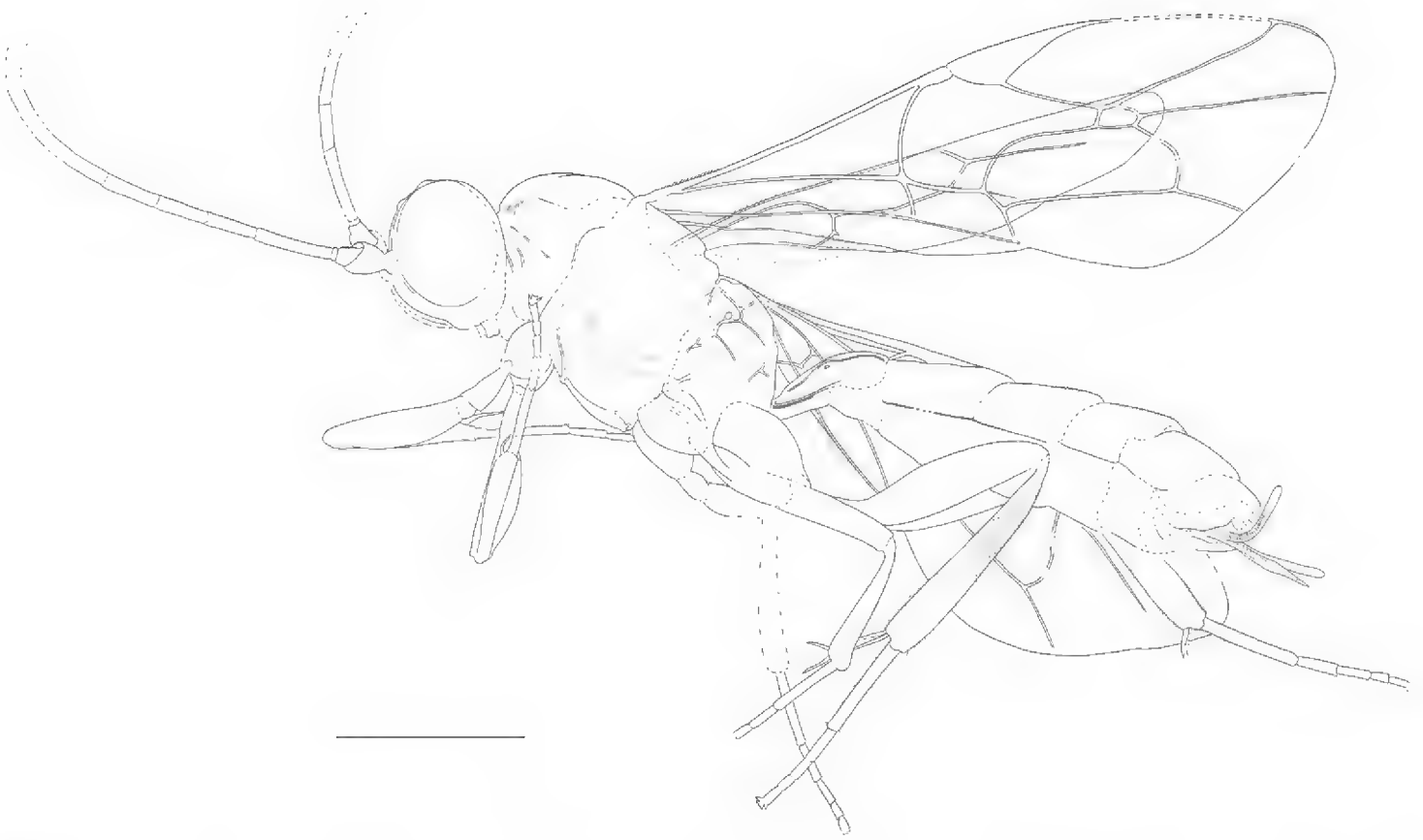

Figure 6. Interpretative line drawing of *Madma oisella* sp. nov. Dotted lines indicate uncertain interpretations. Different detailed photographs were used as templates to create this drawing. Scale bar: 1 mm.

Metasoma. Depressed to cylindrical. S1 reaches around middle of T1, anteriorly with a median keel, centrally with a weak median swelling. Presence of laterotergite 1 unclear; if present then membranous on entire length. T1 in dorsal view about 2–2.5× as long as wide, petiolate, but sides evenly tapering from apex to base as tergite relatively short, in lateral view continuously expanding in profile; spiracle at around 0.6× T1 length in profile; dorso-lateral carina complete, above spiracle; latero-median carinae long, almost reaching posterior margin, parallel to each other; sculpture shagreened or punctured, but could be an artefact. T2 in dorsal view transverse; sculpture if present not strong and even on entire tergite length; latero-median carinae absent; impressions in anterior half either absent or shallow; thyridium present and shape unclear. Dorsal surface of T3 and remaining tergites evenly convex. T3 and T4 with posterolateral corners rounded. S6 unclear, seems transverse with simple apical margin. T7 conspicuously shorter than T6. T8 short, not elongated in horn or boss. Ovipositor sheaths 0.2× metasoma length, parallel-sided, with dense short setae. Ovipositor straight and compressed, parallel sided until tip where dorsal valve expanding into nodus; tip of lower valve with at least four distinct oblique teeth.

Discussion

Why are there so few Oise amber ichneumonids?

In our examined material, we found many more Braconidae than Ichneumonidae. And while ichneumonids seem rare in Oise amber, they are, together with Braconidae, abundant in Baltic amber. For comparison, the Baltic amber collection in Copenhagen

contains about 145 Braconidae and 69 Ichneumonidae, so a ratio of about 2:1 (L. Vilhelmsen, pers. comm.), compared to nearly 20:1 in Oise amber. Although most Ichneumonidae in Baltic amber belong to only six subfamilies, more and more specimens are being described (Manukyan 2019; Manukyan and Zhindarev 2021). Even in the Cretaceous Taimyr amber, braconids and ichneumonids are found in very similar proportions (D. Kopylov, pers. comm.). Therefore, it is surprising that we found so few Ichneumonidae in Oise amber, while Braconidae are rather abundant.

There are many reasons why some organisms could get stuck more easily in one amber than in another. Entrapment in different ambers could differ because of resin viscosity, behaviour of the insect, habitat requirements, or how fast the tree produces resin (Martinez-Delclos et al. 2004). The major difference that may partially explain these different ratios is the size of the amber pieces which are, in general, much smaller for Oise amber. Indeed, it is rare to find Oise amber pieces exceeding a few centimetres while most of the Baltic amber ones are several centimetres long. Additionally, the most fossiliferous Oise amber pieces are, for the most part, the result of relatively thin vertical flows in which the insects are trapped between successive flows. As a result, large Ichneumonidae exceeding 10 mm in length are unlikely to be trapped in this type of resin flow. This directly results in a bias with larger specimens able to free themselves from the fresh resin.

While small ichneumonids may be trapped inside a small fresh resin flow, the big ones need more than just one flow of resin to be entirely covered and are exposed to predation during that time (Martinez-Delclos et al. 2004). A similar bias regarding size is also recorded in other Hymenoptera or insect lineages found in Oise amber (Brasero et al. 2009). In fact, the lineages with relatively large representatives are rarely found (e.g., Odonata) or only partially preserved since one amber fragment is not sufficient to preserve the entire specimen. However, the size bias does not explain the difference compared to Taimyr amber, which also is preserved only in very small pieces. And since Cheloninae (Braconidae) are similar in size to many Ichneumonidae and were found more frequently in our studied material, body size does not seem to be the main cause, or for sure not the only one, for our observed braconid/ichneumonid ratio.

A different behaviour between Eocene ichneumonids and braconids could explain the different ratio between the two families. However, this is clearly difficult to examine. Habitat, as another possible reason, seems less probable, since both groups mostly share habitats and have today similar distributions and hosts. However, there is still a lot of unstudied Oise amber in the collection of the MNHN, and the ratio between the two families could still change with further examination.

Advantages of preservation in amber

While compression fossil localities are on average older than amber deposits, amber fossils often give us a more complete picture of the morphology of specimens and thus allow us to place them more accurately. Although the earliest ichneumonids were described from compression fossils, a lot of information about the past ichneumonid subfamily diversity comes from amber (Kasparyan 1988; Manukyan and Zhindarev 2021).

From 31 amber species described, many belong to extinct subfamilies, which were newly described and often uniquely present in amber. Although preferential preservation of small ichneumonids in amber partly explains its unique subfamily composition, the more complete preservation compared to the compression fossils might play a role, too. In the recently published morphological matrix with 222 characters, up to 64% of characters could be scored in amber fossils, compared to only 38% in compression fossils (Spasojevic et al. 2021). We estimate that an even higher percentage of those characters (around 70%) could be scored for our fossils from Oise amber. In contrast, the amount of missing data in compression fossils is often so big that the fossils must be labelled as *incertae subfamiliae* (Spasojevic et. al 2018a, b; Klopfstein and Spasojevic 2019), which suggests that characters for identifying new subfamilies might be rarely preserved.

Not only the amount of missing data is different in amber compared to compression fossils, but also the type of the preserved characters varies (Grimaldi et al. 1994). Due to the chitinous exoskeleton, we usually do not see any inner structures in ichneumonid compression fossils. However, in amber, the remains of insects can become translucent, revealing inner structures. As this is often happening in Oise amber we were, for example, able to see inside the head of *P. eocenicus*, which was occupied by large vessels below each antenna, which might be tracheal air sacs, and a solid structure behind the clypeus, which could correspond to the muscles of the sucking pump. Further examination of Oise amber fossils, both by light microscopy and micro-CT scanning, will certainly reveal many more internal structures in Oise insects (Kehlmaier et al. 2014).

Difficulties in placing fossil ichneumonids

All three species discussed in this paper exhibit several plesiomorphic characters in combination with more derived characters, making it difficult to decide on stem versus crown group placements. They share the complete propodeal carination, which is characteristic of all Cretaceous subfamilies (Kopylov 2009; 2010a, b; 2012), and possibly also of the earliest representatives of many extant subfamilies, which have subsequently lost some of the carinae (for a discussion on Pimplinae, see Kopylov et al. 2018). In addition, *M. oisella* has a wide, oblique and pentagonal areolet, which is rare among extant ichneumonids (present only in Labeninae), but occurs in many Cretaceous fossils and *Albertocryptus dossenus* that, although placed in Labeninae, was recovered within Ichneumoniformes in a total-evidence analysis (Santos et al. in press). *Pappous trichomatius* and *Palaeometopius eocenicus* both have a broad, subquadrate T1 with long latero-median carinae, which is present in the oldest ichneumonids, Palaeoichneumoninae, and in Labenopimplinae. Therefore, the derived characters, such as the petiolate T1 and bilobed posterior transverse carina on the mesosternum in *M. oisella*, and the setose eyes in *P. trichomatius*, are not enough to clearly place them in crown Phygadeuontinae and crown Tryphoninae, respectively. Finally, the crown group placement of *P. eocenicus* is also questionable, as the most similar extant Tryphoninae do not have a long ovipositor, another plesiomorphic character.

One of the reasons why it is so difficult to distinguish stem from crown groups in ichneumonids is the high prevalence of homoplastic characters (Gauld and Mound 1982) which do not reflect a common ancestry, but rather ecological similarities between groups. However, the problem is not unique to ichneumonids and not only a consequence of a wrong interpretation of homologies, but also of characters in fossil and taphonomic processes (Donoghue and Purnell 2009). The "stem versus crown" distinction became especially important with the advent of node dating, where a wrong interpretation of fossil position leads to erroneous divergence time estimates (Parham et al. 2012; Warnock et al. 2015). A stem group fossil wrongly interpreted as crown group, and thus used to constrain the minimum age of its most recent common ancestor, will directly lead to age estimates which are too old. Sometimes even correctly identified stem fossils are erroneously used to calibrate the age of crown groups. One solution to the problem is a more careful naming of newly described fossils, by expressing the uncertainty in their placement in a prominent place, for instance using the open nomenclature framework (Matthews 1973). Furthermore, palaeontologists should avoid naming fossils after extant genera when the subfamily placement is unclear, in order to avoid future confusion when a placement is revised, as in *Palaeometopius* now removed from Metopiinae. In addition, one can make use of total-evidence dating methods which do not require prior placement of fossils, but rather use morphological information to infer them (Ronquist et al. 2012).

Lessons for morphological phylogenetics

Our analyses of three Oise amber fossils have demonstrated the difficulties associated with integrating fossils into the modern classification. In the end, only a phylogenetic view on fossil placement can deliver the full picture, as higher classification always somewhat blurs the true relationships, especially where stem lineages are concerned. However, morphological phylogenetic analyses suffer from issues concerning assumptions about character evolution and might thus find erroneous relationships, although Bayesian methods apparently show improvements over parsimony-based techniques (O'Reilly et al. 2016). Importantly, model-based approaches allow testing of scenarios for character evolution and even methods for character coding against one another and thus facilitate their critical evaluation (e.g., Wright et al. 2016; Klopfstein and Spasojevic 2019).

The high prevalence of plesiomorphic character states found in this study, most of which are already present in the Cretaceous subfamilies, indicates that the commonly used stationary models of character evolution (Lewis 2001) might be misleading in Ichneumonidae morphology. Such models assume that evolution had reached its steady state already at the root of the tree of the taxa analysed; at least for areolet shape and propodeal carination, the Oise fossils indicate that this might not be the case. Although sample size is of course rather small, it counts several times when fossils are included alongside extant taxa to learn about character evolution (e.g., Coiro et al. 2018). In Hymenoptera, it was demonstrated that inclusion of fossils strongly enhances the signal of directional evolution of wing venation and sclerite fusion, and that

a non-stationary model of morphological evolution can capture this signal (Klopfstein et al. 2015). The use of such models should be evaluated in the future for ichneumonid phylogenetics, at least for the aforementioned character systems.

Outlook

By describing two new ichneumonid specimens belonging to two new genera, and redescribing *Palaeometopius eocenicus* from Oise amber, we added crucial information and detailed morphological insights to the ichneumonid fossil record in amber. Fossils from the subfamilies Tryphoninae and Phygadeuontinae have been found before, but mostly as compression fossils and from the Late Eocene or younger. This makes *Madma oisella*, *Pappous trichomatius* and *Palaeometopius eocenicus* some of the oldest representatives of those subfamilies.

In this study we highlight the general difficulty of placing fossil species, mainly because they are much older and belong to stem lineages or even extinct side branches. Only a phylogenetic analysis can potentially resolve this issue and lead to a more adequate classification. The newly described fossil species, which are important representatives of early Tryphoninae and Phygadeuontinae, with their highly detailed preservation, will be added to the already existing morphological matrix of Spasojevic et al. (2021). Thus, their high number of coded characters will most certainly add useful information for future phylogenetic analyses integrating fossil and extant taxa.

By describing and carefully classifying new fossil ichneumonid species, we can improve the understanding of the diversity and species composition of this very species-rich group of parasitoids through time. Many inclusions in Oise amber remain unchecked and more ichneumonid specimens, probably including some from extant subfamilies, could be discovered. It remains unclear why there are only extinct subfamilies in the Cretaceous and only extant subfamilies in the Paleogene. It is therefore crucial to continue describing fossils and investigate deposits (e.g., Menat in France) from the time around the K-Pg boundary, to help us understand how the subfamilies evolved and what happened with them during the mass extinction event 66 million years ago.

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of *Pappous trichomatius* and *Madma oisella*. A great thanks also to Dmitri Kopylov and Davide Dal Pos for their constructive comments and feedback in their review, which greatly improved our manuscript.

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